# Are mangroves important for reef fish on Mayotte Island (Indian Ocean)?

by

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**Key words**
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**Abstract**. – In order to understand the potential role of the mangroves of Mayotte Island for reef fishes, sampling was conducted monthly from April 2016 to April 2017 in three sites along a mangrove fringe: Bandrélé near fringing reef, Dzoumogné close to a river mouth and Malamani in a bay. Fishes were sampled using a fyke-net combined with visual census surveys (UVC) and eight environmental variables were recorded at each site to determine their relationship with the fish community structure. A total of 992 individuals reef fishes distributed among 44 species were recorded. Considering the sampling methods, 869 individuals comprising 35 species were observed by UVC and 123 individuals belonging to 25 species were captured with a fyke-net. Samples were mainly composed of juvenile fishes, whether 81% and 93.5% in relative abundance for UVC and catches, respectively. Whatever the sampling method, fish abundance and species richness were significantly higher in the Bandrélé mangrove. Overall, six species (*Abudefduf sparoides*, *A. vaigiensis*, *Acanthurus blochii*, *Lutjanus fulviflamma*, *L. monostigma* and *Sphyraena barracuda*) were dominant and accounted for 59% of total number of fish observed and captured. Species richness and fish abundance showed a seasonal variation for UVC and were significantly higher in wet season (November-April) with one important peak in January. Canonical RDA analysis revealed that the most significant factors explaining the distribution of fish community structure were temperature, reef proximity and fishing time for the catches, and temperature, water transparency and reef proximity for UVC. Temperature appears to be the most important factor explaining the seasonal variation, while spatial variation of reef fish abundance in mangrove may be related to reef proximity, water transparency and fishing time. First order carnivores, zooplanktivores and herbivores were mainly observed in Bandrélé, whereas piscivores were dominant in Malamani mangrove for both methods. Second order carnivores were well represented in Dzoumogné site. We propose that water transparency due to reef proximity with high salinity level and food availability were probably the most important factors structuring reef fish community in the mangrove. Moreover, the importance of Mayotte mangroves for reef fishes appears to relate to site, environmental variables and seasonal factor. Notwithstanding the important role of mangroves for several species, its role of nursery for reef fish should not be generalised.

**Résumé**. – Les mangroves sont-elles importantes pour les poissons récifaux de l'île de Mayotte (océan Indien) ?

Les habitats côtiers peu profonds tels que les mangroves sont largement considérés comme des zones de nurseries importantes pour diverses espèces de poissons récifaux. Dans les Caraïbes, les mangroves sont clairement reliées aux récifs coralliens, tandis que la fonction des mangroves comme nurserie pour les poissons récifaux dans la région de l'Indo-Pacifique reste encore débattue. Cet écosystème est malheureusement affecté par diverses activités humaines telles que le développement côtier, le défrichage et des pratiques de pêche non durables. Pour les poissons des récifs coralliens de l'île de Mayotte dans l'océan Indien, il était donc essentiel de comprendre le rôle joué par les mangroves afin de mieux gérer cet écosystème qui est encore mal perçu. Trois sites (Bandrélé près d'un récif frangeant, Dzoumogné près d'une embouchure de rivière et Malamani dans une baie) ont fait l'objet d'un échantillonnage mensuel d'avril 2016 à avril 2017. Sur chaque site, l'échantillonnage des poissons a été réalisé à l'aide d'un verveux combiné à des comptages visuels (UVC) ainsi qu'à un enregistrement de huit variables du milieu afin de déterminer leurs relations avec la structure de la communauté de poissons. Nous avons identifiés 992 poissons appartenant à 44 espèces. Considérant les méthodes d'échantillonnage, 869 individus de 35 espèces ont été observés et 123 individus de 25 espèces ont été capturés. En abondance relative, les échantillons sont majoritairement composés de poissons juvéniles pour les observations (81%) et pour les captures (93,5%). Quelle que soit la méthode d'échantillonnage, l'abondance du poisson et la richesse spécifique sont significativement plus fortes dans la mangrove de Bandrélé. Dans l'ensemble, six espèces (*Abudefduf sparoides*, *A. vaigiensis*, *Acanthurus blochii*, *Lutjanus fulviflamma*, *L. monostigma* and *Sphyraena barracuda*) sont dominantes et représentent 59% du nombre total de poissons observés et capturés. La richesse spécifique, ainsi que l'abondance, montrent une variation saisonnière pour les observations et sont significativement plus élevées pendant la saison humide (novembre à avril) avec un pic important en janvier. L'analyse canonique des redondances (ACR) révèle que les facteurs les plus significatifs expliquant la distribution de la structure de la communauté de poissons sont la température, la transparence de l'eau et le temps de pêche pour les captures ainsi que la température, la transparence de l'eau et la proximité des récifs pour les observations. La température semble donc être le facteur le plus important expliquant la variation saisonnière, tandis que la variation spatiale de l'abondance dans la mangrove peut être liée à la proximité des récifs, à la transparence de l'eau et au temps de pêche. Les poissons macrocarnivores (C1), les zooplanctivores et les herbivores sont principalement observés à Bandrélé, alors que les piscivores dominent la mangrove de Malamani et que les microcarnivores (C2) sont bien représentés à

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Dzoumogné. Nous proposons que la transparence de l'eau due à la proximité des récifs avec une salinité élevée et la disponibilité en nourritures soient les facteurs les plus importants qui pourraient expliquer la structuration de la communauté de poissons récifaux dans les mangroves de Mayotte. Néanmoins, comme l'importance des mangroves à Mayotte pour les poissons récifaux semble être liée aux sites, aux variables environnementales et au facteur saisonnier, malgré le rôle important des mangroves pour plusieurs espèces, leur rôle de nurserie pour les poissons récifaux ne devrait pas être généralisé à l'ensemble de l'écosystème mangrove de l'île.

## INTRODUCTION

In many studies around the world, tropical shallow coastal habitats are known to play important ecological roles for fish communities as nurseries. Among these habitats, mangrove ecosystems are widely considered as an important habitat for juveniles of various reef fish species (Parrish, 1989; Beck *et al.*, 2001; Laegdsgaard and Jonhson, 2001; Nagelkerken *et al.*, 2002; Mumby *et al.*, 2004; Kimirei *et al.*, 2011). According to Beck *et al.* (2001), the ecological processes operating in nursery habitats must support greater contributions to adult recruitment from any combination of four factors: (1) density, (2) growth, (3) survival of juveniles, and (4) movement to adult habitats. Mangrove ecosystems appear to offer an attractive habitat for early life-stage of many fish species. Several hypotheses have been proposed to explain the high abundance of juvenile fish species in these habitats. Mangroves are attractive for juveniles because they may intercept planktonic fish larvae more effectively compared to coral reefs (Parrish, 1989). Moreover, the structural complexity of mangroves provides excellent shelter against predators (Parrish, 1989; Robertson and Blaber, 1992; Laegdsgaard and Johnson, 2001; Cocheret de la Morinière *et al.*, 2004; Nanjo *et al.*, 2011). Other factors, such as the relatively high turbidity of waters within mangroves, decrease the foraging efficiency of predators (Robertson and Blaber, 1992; Benfield and Minello, 1996). Finally, these habitats provide a high abundance of nutrients and food for juvenile fishes (Laegdsgaard and Johnson 2001; Lugendo *et al.*, 2006; Nagelkerken, 2009). Consequently, the main explanations for the nursery role of mangrove are the predation risk hypothesis and the food availability hypothesis. Juveniles can reduce the risk against predation by larger fish by entering the structural complexity of mangroves roots; moreover, there is greater availability of food in mangroves compared to adjacent habitats (Laegdsgaard and Johnson 2001).

More peculiarly, the function of the Indo-Pacific mangroves as nursery habitats for coral reef fishes is still a matter of scientific debate (Thollot and Kulbicki, 1988; Thollot, 1992; Laroche *et al.*, 1997; Kimirei *et al.*, 2011; Honda *et al.*, 2013; Paillon *et al.*, 2014), while in the Caribbean, mangroves have been recognized as important nursery habitats of several coral reefs species (Nagelkerken *et al.*, 2000a; Cocheret de la Morinière *et al.*, 2002; Nagelkerken and Van der Velde, 2002; Dorenbosch *et al.*, 2004a). Due to a very different environmental context of Indo-Pacific with regard to the Caribbean, our understanding of the nursery role of these habitats in this region remains insufficient (see Nagelkerken, 2009).

The importance of mangroves for coral reef fishes may also vary depending on the species, environmental factors and biogeographic region. For example, in the Caribbean, mangroves are permanently inundated, thus facilitating the accessibility to this habitat for juvenile fishes (Nagelkerken, 2007; Unsworth *et al.*, 2007). Tidal ranges are often high in large parts of the Indo-Pacific region and mangroves can commonly be alternately flooded or exposed during tidal cycle. At high tide, fishes move into the mangroves to feed or shelter and out onto adjacent seagrass beds at low tide (Dorenbosch *et al.*, 2004b; Lugendo *et al.*, 2006). The large tidal ranges in the Indo-Pacific region are important in structuring fish assemblages in mangrove systems and determine connectivity with other intertidal habitats (Dorenbosch *et al.*, 2004b; Unsworth *et al.*, 2007; Olds *et al.*, 2012). Also, salinity has been reported to be an important factor influencing fish assemblages, especially in estuarine environments where fish communities are often structured in accordance with local salinity gradients (Barletta *et al.*, 2005). Other environmental factors like temperature, turbidity and spatial variables (reef and river proximity) are known to structure fish communities (Benfield and Minello, 1996; Dorenbosch *et al.*, 2004a; Lugendo *et al.*, 2007; Vaslet *et al.*, 2010).

Finally, several studies have shown a decrease in global surfaces of the mangroves due mainly to anthropogenic damage and climate change (Valiela *et al.*, 2001; Alongi, 2002, 2008; Duke *et al.*, 2007). This situation also highlighted the need for more studies in the Indo-Pacific region on the fish communities of mangroves for a better understanding of the role of these ecosystems to assess the risk of the loss of habitat and to guide the decision of local managers. At a local scale, Mayotte mangrove surfaces have diminished overall by about 5% over the period 1950-2011 due to strong demographic and development pressures of island (Jeanson *et al.*, 2014). To date, no study has looked at the importance of mangroves for coral reef fishes at Mayotte Island. The present study was conducted to determine the composition of reef fish communities inhabiting mangroves in order to relate the spatial organisation of fish assemblages to environmental descriptors and evaluate the functions provided by these ecosystems for reef fishes in Mayotte.

## MATERIALS AND METHODS

### Study area

Mayotte Island is situated approximately 400 km northwest of Madagascar and about 500 km east of the African coasts in the Western Indian Ocean (Fig. 1). This island is almost entirely surrounded by a 197 km barrier reef, with a large lagoon of 1500 km$^2$, one of the largest reef lagoons in the Indian Ocean. The mangrove total coverage represented 703 ha in 2011 (Jeanson *et al.*, 2014); it is nearly 30% of the shoreline of Mayotte. Mayotte presents tides that are semidiurnal and ranged between 0 and 4 m with a mean spring range of about 3.2 m. Thus, mangroves are commonly being flooded or exposed during the tidal cycle.

Three sites were sampled (Fig. 1): (1) Dzoumogné in the north is the second largest mangrove stand of Mayotte with an area of 107 ha in 2011 (Jeanson *et al.*, 2014). The sampling site was located close to one of the permanent river mouths and characterized by high turbidity and mudflats. This site is considered to be affected by anthropogenic impacts (*e.g.* waste discharges, fishing practice, cutting mangroves). It is at a distance of ~1 km from a small fringing coral reef. (2) Bandrélé in the southeast was characterized by moderate areas of mangrove forest (37 ha) in 2011 (Jeanson *et al.*, 2014), sandy substrates, clear water and situated at a distance (0.4 km) from a well-developed reef. There is one nonpermanent river at the beginning of Bandrélé village at 0.8 km in the south of sampling site. Finally (3), in the southwestern of the island, Malamani mangrove of Bouéni Bay is the largest mangrove stand in Mayotte (186 ha in 2011) (Jeanson *et al.*, 2014). This bay was characterized by a muddy substratum, small rivers that discharge in this area during the rainy season, domestic pretreated wastewater (Herteman *et al.*, 2011) and it is far from the reef (about 1.5 km to 2 km).

### Sampling methods

The present study was conducted monthly from April 2016 to April 2017 along the mangrove fringe. Fish in mangroves were sampled using one small fyke-net combined with underwater visual census (UVC) two hours after high tide. The fyke-net measured 12.5 m long and was composed by two 4.5 m wings and 1.8 m height with 10 mm mesh size and multiple creels 6 mm mesh size, 0.4 m in diameter, ending with a pocket of 2.9 m. The water depth along the mangrove fringe reached 2 m during high tide and was completely exposed during low tide. Passive fishing gears such as fyke-nets are well adapted to sample smaller mangrove fish (Louis *et al.*, 1992), while UVC is appropriate for surveying large mobile species in mangroves with sufficient water clarity (> 1 m). Each site was sampled every two weeks to meet the same tide coefficient and to have high tide in the morning. To survey fish, 30 to 45 minutes censuses were performed by snorkelling at each site on both sides of the fyke-net, covering approximately 250 m$^2$. The observer moved slowly throughout mangrove roots, and all fishes within the area were counted and photographed for later identification. At each site, fyke-net was always settled in front of the mangrove border so opening face landward and removed 1 h 30 later at low tide. All fish captured were brought back to the

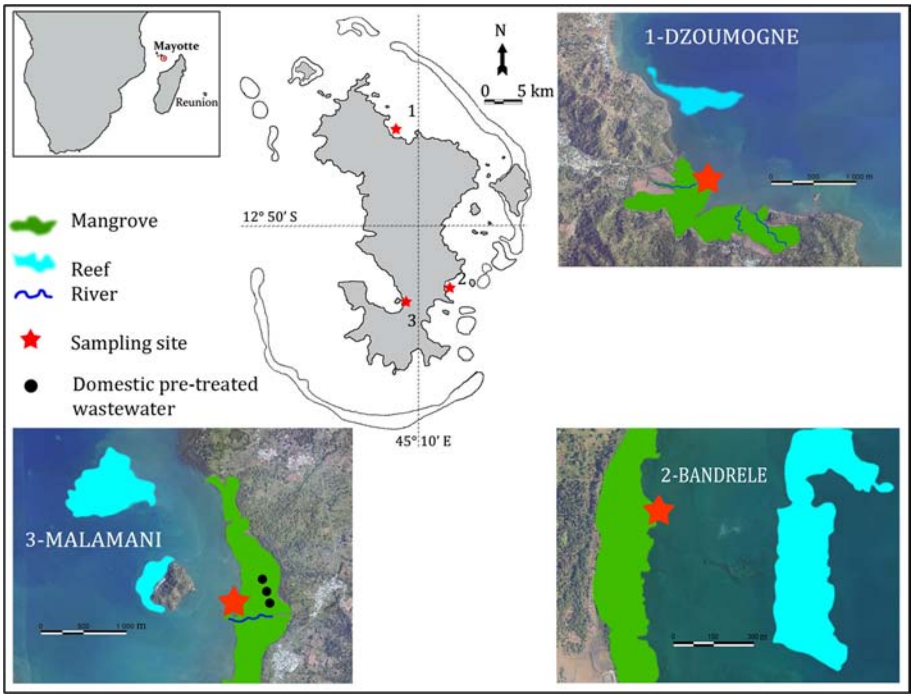

Figure 1. – Location of the three sampling sites in the lagoon along the eastern coast and south-western coast of Mayotte Island. The numbers refer to the text where further information is found to describe each location.

Table I. – Family and species name sampled in the three mangrove habitats (Band= Bandrélé, Dzou= Dzoumogné, Mala= Malamani) and the species codes used in RDA (Fig. 6) are given. Their maximum length was obtained from the Sea Fishes book (Smith and Heemstra, 1986) and FishBase World Wide Web (Froese and Pauly, 2017). Trophic categories (TC): Pi, Piscivores; C1, First order carnivores; C2, Second order carnivores; Z, Zooplanktivores; He, Herbivores. Dominant stages of fishes (J = juvenile, A = adult) and sampling method (SM): V = UVC, F = fyke-net are added.

| Families | Species | L. max | Species code | Dominant stage | Band | Dzou | Mala | TC | SM |
|---|---|---|---|---|---|---|---|---|---|
| Synodontidae | *Saurida gracilis* (Quoy & Gaimard, 1824) | 32 | Sagra | J-A | x |  | x | Pi | V-F |
| Bothidae | *Bothus pantherinus* (Rüppell, 1830) | 39 | Bopan | J | x |  |  | C2 | F |
| Belonidae | *Tylosurus crocodilus* (Péron & Lesueur, 1821) | 135 | Tycro | J | x | x | x | Pi | V-F |
| Diodontidae | *Diodon hystrix* (Linnaeus, 1758) | 91 | Dihys | A | x | x | x | C2 | V |
| Tetraodontidae | *Arothron immaculatus* (Bloch & Schneider, 1801) | 30 | Arimm | A-J | x | x | x | C1 | V-F |
|  | *Arothron* spp. | – | Arosp | A |  | x | x | C1 | V |
|  | *Canthigaster solandri* (Richardson, 1845) | 11 | Casol | J | x | x |  | C2 | F |
| Monacanthidae | *Monacanthidae* spp. | – | Monac | J |  | x |  | C2 | F |
| Balistidae | *Balistoides viridescens* (Bloch & Schneider, 1801) | 75 | Bavir | A |  |  | x | C1 | V |
| Scorpaenidae | *Pterois miles* (Bennett, 1828) | 35 | Ptmil | A |  |  | x | Pi | V |
| Serranidae | *Epinephelus lanceolatus* (Bloch, 1790) | 270 | Eplan | J |  |  | x | Pi | F |
|  | *Epinephelus malabaricus* (Bloch & Schneider, 1801) | 234 | Epmal | J | x |  | x | Pi | F |
|  | *Epinephelus ongus* (Bloch, 1790) | 40 | Epong | A | x |  |  | C1 | V |
| Echeneidae | *Remora* spp. | – | Remor | J |  |  | x | C2 | F |
| Lutjanidae | *Lutjanus argentimaculatus* (Forsskål, 1775) | 120 | Luarg | J-A | x |  | x | C1 | V-F |
|  | *Lutjanus ehrenbergii* (Peters, 1869) | 35 | Luehr | J | x | x |  | C1 | V-F |
|  | *Lutjanus fulviflamma* (Forsskål, 1775) | 35 | Luful | J-A | x | x | x | C1 | V-F |
|  | *Lutjanus fulvus* (Forster, 1801) | 35 | Lufvu | J-A | x | x | x | C1 | V-F |
|  | *Lutjanus monostigma* (Cuvier, 1828) | 60 | Lumon | J | x |  |  | C1 | V-F |
|  | *Lutjanus rivulatus* (Cuvier, 1828) | 80 | Luriv | J | x |  |  | C1 | V-F |
|  | *Lutjanus russelli* (Bleeker, 1849) | 50 | Lurus | J | x |  |  | C1 | V |
|  | *Lutjanus* spp. | – | Lutsp | J | x |  |  | C1 | F |
| Haemulidae | *Plectorhinchus gibbosus* (Lacepède, 1802) | 70 | Plgib | J-A | x | x |  | C1 | V-F |
| Lethrinidae | *Lethrinus harak* (Forsskål, 1775) | 40 | Lehar | A-J | x |  | x | C2 | V |
| Mullidae | *Parupeneus* spp. | – | Mulsp | J |  | x |  | C1 | F |
|  | *Parupeneus barberinus* (Lacepède, 1801) | 50 | Pabar | J | x |  |  | C1 | V |
|  | *Parupeneus ciliatus* (Lacepède, 1802) | 35 | Pacil | J | x |  |  | C1 | F |
| Kyphosidae | *Kyphosus cinerascens* (Forsskål, 1775) | 45 | Kycin | J | x |  |  | Z | V |
| Chaetodontidae | *Chaetodon auriga* (Forsskål, 1775) | 23 | Chaur | A-J | x |  |  | C2 | V |
|  | *Chaetodon lunula* (Lacepède, 1802) | 20 | Chlun | J-A | x |  |  | C2 | V-F |
| Pomacentridae | *Abudefduf septemfasciatus* (Cuvier, 1830) | 23 | Absep | A-J | x |  |  | Z | V |
|  | *Abudefduf sexfasciatus* (Lacepède, 1802) | 19 | Absex | J | x |  |  | Z | V |
|  | *Abudefduf sparoides* (Quoy & Gaimard, 1825) | 16 | Abspa | J | x |  |  | Z | V |
|  | *Abudefduf vaigiensis* (Quoy & Gaimard, 1825) | 20 | Abvai | J | x |  | x | Z | V-F |
|  | *Chrysiptera unimaculata* (Cuvier, 1830) | 10 | Chuni | J-A | x |  |  | Z | V |
| Labridae | *Halichoeres cosmetus* (Randall & Smith, 1982) | 13 | Hacos | A |  | x | x | C2 | V |
| Ephippidae | *Platax orbicularis* (Forsskål, 1775) | 40 | Plorb | J-A | x |  | x | C2 | V-F |
| Siganidae | *Siganus* spp. | – | Sigsp | J | x | x | x | He | V-F |
|  | *Siganus sutor* (Valenciennes, 1835) | 45 | Sisut | J | x |  |  | He | V |
| Zanclidae | *Zanclus cornutus* (Linnaeus, 1758) | 23 | Zacor | J-A | x |  |  | C2 | V |
| Acanthuridae | *Acanthurus blochii* (Valenciennes, 1835) | 40 | Acblo | J | x |  |  | He | V-F |
|  | *Acanthurus triostegus* (Linnaeus, 1758) | 25 | Actrio | J-A | x |  |  | He | V |
| Sphyraenidae | *Sphyraena barracuda* (Edwards, 1771) | 170 | Spbar | J-A | x | x | x | Pi | V-F |
|  | *Sphyraena chrysotaenia* (Klunzinger, 1884) | 32 | Spchr | A |  |  | x | Pi | F |

laboratory where they were sorted, identified, measured and counted. Individual fishes were identified to species level as much as possible using the Sea Fishes book (Smith and Heemstra, 1986). Fishes were recorded as adults or juveniles on the basis of body size and colour, and their total length (TL) was estimated to the nearest centimetre. Fishes were recorded as juveniles when they were smaller than 1/3 of the maximum species length (Nagelkerken and Van der Velde, 2002). Maximum lengths of species were obtained from the Sea Fishes book (Smith and Heemstra, 1986) and FishBase World Wide Web (Froese and Pauly, 2017). Fish species were classified to five trophic groups based on the main dietary items available in FishBase (Froese and Pauly, 2017): (Pi) piscivores (consuming more than 80% of fishes), (C1) first order carnivores (feeding on large invertebrates), (C2) second order carnivores (feeding on small benthic invertebrates), (Z) zooplanktivores, and (He) herbivores (consuming algae and plants) (Tab. I). Eight quantitative environmental variables were measured before settling the fyke-net in each site. Salinity was measured using a seawater refractometer, and temperature with a digital thermometer for aquarium. Water transparency was measured using a vertical Secchi disk, and depth with a dive computer. A timer controlled the fishing time; tide coefficient was noted with tides tables, and reef and river proximity were measured using Global Positioning System (GPS). These environmental characteristics of each site are summarized in table II.

### Data analyses

Data collected from each site were analysed using a parametric or a nonparametric test for overall species richness and abundance, size distribution for the main species, abundance of each trophic category and juvenile and adult abundance between sites for both sampling techniques. Data was tested for homogeneity of variances using a Fligner-Killeen test and, where necessary, the data was log-transformed to meet the requirements. In case variances were homogeneous, a one-way ANOVA was employed to test differences in both fish community variables and environmental variables between sites. Because assumptions of homogeneity of variance could not be met by some data even after log-transformation, a Kruskal-Wallis test was used as a nonparametric test. Also, monthly variations in abundance, total species richness and environmental variables among seasons (dry and wet season) were analysed with Wilcoxon signed-rank tests. Data treatment and analysis were performed using the R 3.3.2 statistical software (R Development Core Team, 2016).

Canonical redundancy analyses (RDA) were used to examine the relationship between the reef fish assemblages and the environmental descriptors influencing their distribution in different sites for both sampling techniques. This canonical method was used to relate the relationships between the species distribution and to a matrix of environmental variables (Legendre and Legendre, 1998). Abundance data are log transformed before the canonical analyses. Each significant environmental variable to the RDA are selected after a forward selection. The statistical significance ($p < 0.05$) of the effect of each explanatory variable is tested by a Monte Carlo permutation test (999 permutations). RDA analyses were performed using the CANOCO program (ter Braak, 1988). Results of the ordination were projected in correlation triplots. The results of RDA analyses were coupled with hierarchical clustering to identify sites groups from the projection of fish abundance on the canonical triplots for both sampling methods. Clusters were performed with the program XLSTAT 2018.1 and were analysed using Ward algorithm and the Euclidian distance matrix computed from the coordinates of the sites produced by the factorial analysis.

## RESULTS

### Spatial and temporal variation in environmental parameters

Only water transparency varied spatially ($p > 0.001$), while fishing time, tide coefficient, water temperature and salinity did not vary across sites. Highest values for water transparency were recorded in Bandrélé site near fringing reef (0.4 km), whereas lowest values were recorded for the Dzoumogné and Malamani mangroves far from reef (> 1 km). Salinity values did not mark a seasonal variation in all sites where levels remained close to that of oceanic water throughout the sampling period (average 32). The variations in water temperature were significant between seasons in all sites, with water temperature during wet season being significantly higher than those of dry season (Wilcoxon signed-rank test; $p > 0.001$). Significant seasonal variations were

Table II. – Environmental characteristics (mean ± SE) of the three sampling sites.

| Site | Water transparency (m) | Temperature (°C) | Salinity | Distance to coral reef (km) | Distance to the river (m) | Fishing depth (m) | Tide coefficient | Fishing time (min) |
|---|---|---|---|---|---|---|---|---|
| Bandrélé | 170 ± 12.6 | 29.4 ± 0.7 | 32.7 ± 0.6 | 0.4 | 800 | 1.4 ± 0.1 | 73.2 ± 5.1 | 76.7 ± 4.3 |
| Dzoumogné | 52.3 ± 6.0 | 29.0 ± 0.8 | 32.0 ± 0.7 | 1.0 | 50 | 1.4 ± 0.1 | 75.4 ± 3.6 | 73.9 ± 3.9 |
| Malamani | 59.0 ± 12.6 | 29.1 ± 0.7 | 31.8 ± 0.6 | 1.5 | 200 | 1.4 ± 0.1 | 71.5 ± 5.1 | 76.9 ± 4.3 |

also recorded for tide coefficient ($p < 0.05$) and fishing time ($p < 0.01$) in all sites. Highest values were observed during dry season for both environmental variables.

### Structure of fish assemblages

In total, 992 individuals reef fishes, belonging to 44 species in 23 families were recorded in the three sampling sites during the study period (Tab. I). With the sampling methods, 869 individuals comprising 35 species in 20 families were observed from UVC technique. In contrast, fewer reef fishes were captured in mangroves with a fyke-net (123 individuals belonging to 25 species in 16 families). Numerically, the most dominant families of total catches were: Lutjanidae (32.5%), Sphyraenidae (17.1%), Acanthuridae (13.8%), Pomacentridae and Tetraodontidae (5.7% both). From UVC, the most dominant families were: Lutjanidae (31.4%), Pomacentridae (21.6%), Acanthuridae (18.1%), Sphyraenidae (6.3%) and Chaetodontidae (4.5%). In terms of numbers of species per family, the most dominant for catches were: Lutjanidae (8 species, 32%), Pomacentridae (5 species, 20%), Mullidae, Serranidae and Tetraodontidae (3 species respectively, whether 12%). The same trend was observed with UVC method (22.9%, 14.3% and 8.6%, respectively).

Total fish abundance differed significantly between study sites (Kruskal-Wallis $p < 0.05$ for catches and $p < 0.001$ for UVC). Species richness showed significant variability between sites ($p < 0.001$) with UVC, but not with captures. Whatever the sampling methods, fish abundance and species richness were significantly greater in the Bandrélé mangrove. Overall, six species were dominant and accounted for 59% of total number of fish observed: *Abudefduf sparoides*, *A. vaigiensis*, *Acanthurus blochii*, *Lutjanus fulviflamma*, *L. monostigma* and *Sphyraena barracuda*. The remaining fish species represent less than 4% of the total fish abundance. Five species contributed 59% of the total catch: *Abudefduf vaigiensis*, *Acanthurus blochii*, *Lutjanus fulviflamma*, *L. monostigma* and *Sphyraena barracuda*.

### Juvenile – adult abundance and length distribution

There were significant differences between juvenile and adult in total abundance in all sites for catches (Kruskal-Wallis; $p < 0.001$), but not for UVC (Fig. 2). Overall, juveniles composed 81% in relative abundance of total fishes observed in sampling sites and 93.5% of the total catches (Fig. 2). Higher proportion of juveniles was found at Dzoumogné (100% of the total catches); however, adult fishes comprised

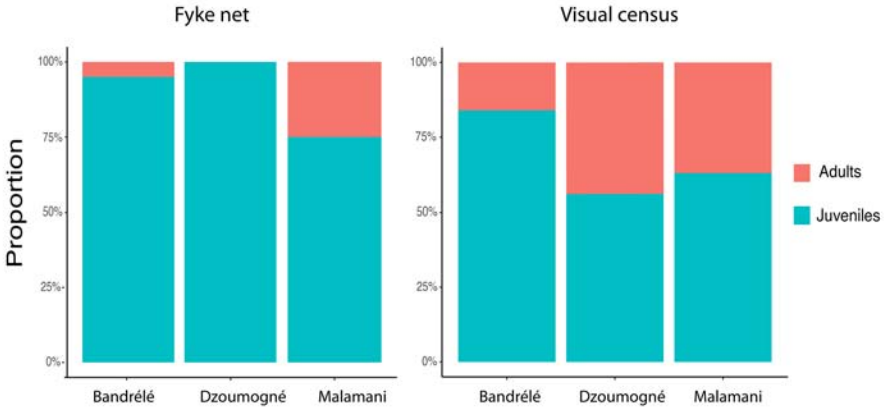

Figure 2. – Relative abundance of adults and juveniles of fishes in different mangrove habitats.

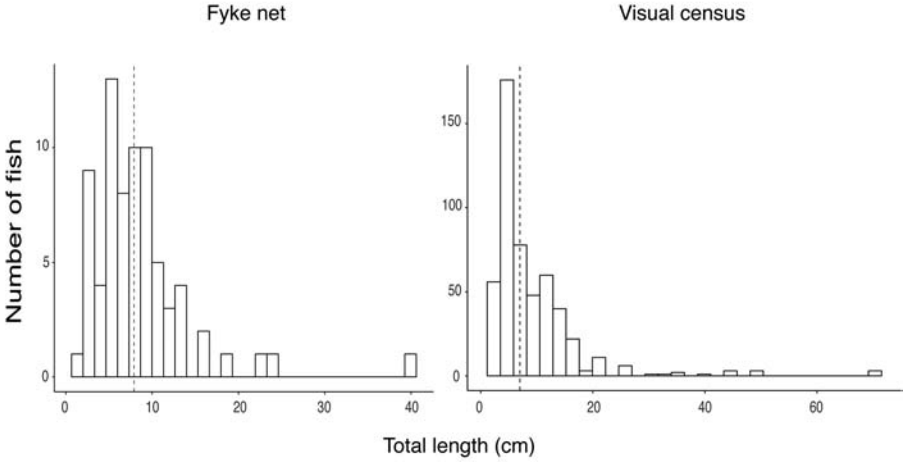

Figure 3. – Size frequency distribution of the main species that contributed 59% of the total fish sampled by both methods. Dashed line indicates median value for each method.

44% and 37.3% at Dzoumogné and Malamani site for UVC method (Fig. 2).

The size frequency distribution of the dominant species from UVC (6 species) and catches (5 species) was analysed (Fig. 3). No difference was found in size frequency distribution of the dominant species from both methods. Value of median and mean fish length was 7 cm and 9.23 cm for UVC and 7.9 cm and 8.44 cm for the catches (Fig. 3). From catches, four species were exclusively represented by juvenile stage: *Abudefduf vaigiensis*, *Acanthurus blochii*, *Lutjanus monostigma* and *Sphyraena barracuda*, while *Lutjanus fulviflamma* showed a proportion of juvenile stage around 82.6%. Only three species (*A. sparoides*, *A. vaigiensis*, *L. monostigma*) were observed 100% in juvenile stage from UVC method. The remaining species exhibited a juvenile proportion of over 75%.

## Trophic categories

The relative proportions of five trophic categories were described in abundance for the three sampling sites (Fig. 4). There was a significant difference in the abundance of first order carnivores between sites (Kruskal-Wallis; p = 0.011 for catches), but no difference was found for the remaining trophic categories. The catches were dominated in relative abundance by first order carnivores in Bandrélé (44.3%) and Dzoumogné (46.3%), while piscivores proportion was greater in Malamani (60%). The first order carnivores were also more diverse (16 species) and more abundant compared to piscivores, which were represented only by seven species. Zooplanktivores were mainly captured in Bandrélé site and represented (8%) in relative abundance (Fig. 4). For these three feeding guilds, they were represented by dominance of a single species (*Lutjanus fulviflamma*, *Sphyraena barracuda*, *Abudefduf vaigiensis,* respectively). The remain-

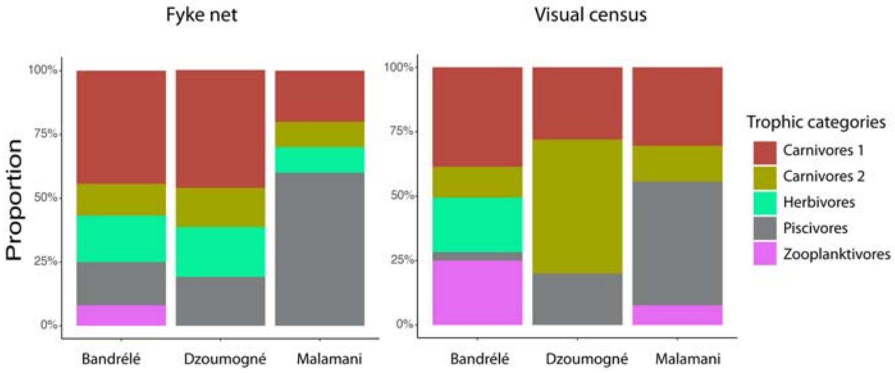

Figure 4. – Relative abundance of the five trophic categories among the three mangrove habitats for fyke-net and visual census.

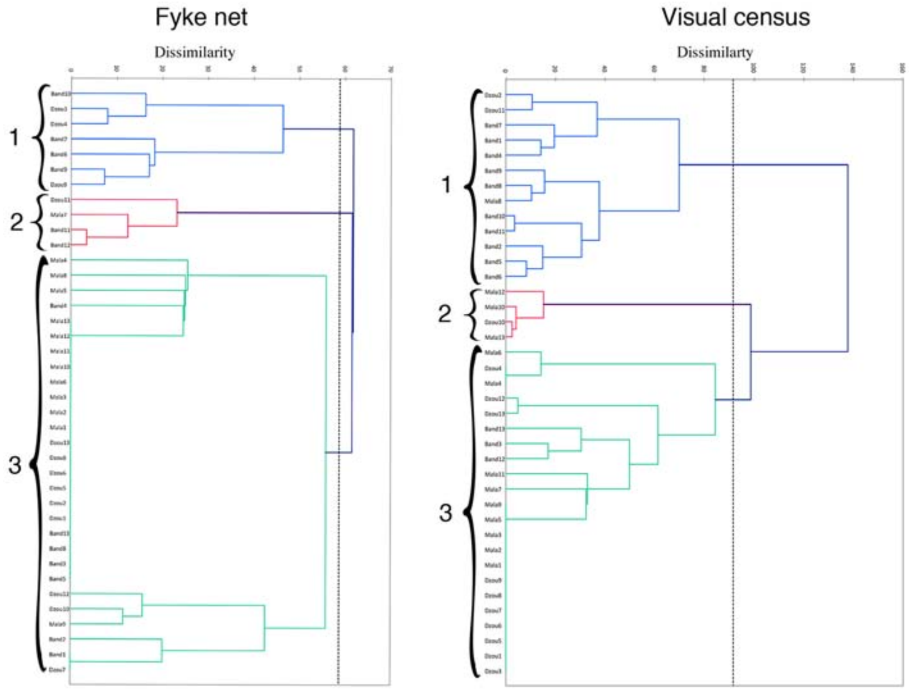

Figure 5. – Hierarchical clustering analysis showing the spatial repartition of 13 sampling months based on fish abundance data for both methods. Sites are coded according to their abbreviation followed by month number, beginning in April (1) and finishing in April again (13). Clusters are separated using Ward algorithm.

ing trophic categories show the same proportion for each site. First order carnivores, zooplanktivores and herbivores were observed in significantly greater numbers in Bandrélé compared to the others sites (Kruskal-Wallis; $p = 0.016$, $p = 0.001$, $p = 0.007$, respectively). Piscivores were poorly represented in Bandrélé. Conversely, an increase in the proportion of first order carnivores, zooplanktivores and herbivores was observed in Bandrélé (Fig. 4). The proportion of second order carnivores was relatively important in Dzoumogné (52% in relative abundance) and dominated by *Halichoeres cosmetus*.

Similar to catch data, the proportion of piscivores was well represented in the Malamani site for UVC (48.1%), with one species dominating the observations (*Sphyraena barracuda*).

### Relationships between fish assemblages and environmental variables

Hierarchical classifications for both sampling methods performed on fish abundance and sampling month divided the sites into three groups (Fig. 5). For catches, the first group was composed by four sampling months of Bandrélé (September, October, December and January) and three months of Dzoumogné (June, July and December). The second group was represented by two months of Bandrélé (February and March), one month of Dzoumogné (February) and one month of Malamani (October). The third group gathered mainly sampling month of Malamani (12 months) followed by Dzoumogné (9) and Bandrélé (7). The highest values of abundance and fish species richness were found in the sampling months of the first and second group, while the third group was less abundant and diverse.

Table III. – Results of the RDA performed on fish abundance. Significant factors were selected using backward permutation tests (number of permutations = 999). The robustness of the analysis was tested using a Monte-Carlo test, NS = non-significant variables.

| Environmental variables | Fyke net | | Visual census | |
|---|---|---|---|---|
| | Abundance | | | |
| Temperature | $p = 0.05$ | | $p = 0.004$ | |
| Salinity | NS | | NS | |
| Water transparency | NS | | $p = 0.002$ | |
| Reef proximity | $p = 0.003$ | | $p = 0.036$ | |
| Fishing depth | NS | | NS | |
| Distance to the river | NS | | NS | |
| Fishing time | $p = 0.011$ | | NS | |
| Tide coefficient | NS | | NS | |
| Canonical axes | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Eigenvalues | 0.120 | 0.064 | 0.204 | 0.056 |
| Species-environment correlations | 0.743 | 0.657 | 0.880 | 0.785 |
| Percentage of variance | | | | |
| Of species data | 12 | 18.5 | 20.4 | 26 |
| Of species-environment correlations | 45.4 | 69.8 | 55 | 70.1 |
| Sum of all canonical eigenvalues | 0.265 | | 0.371 | |
| Significance of first canonical axis | 0.046 | | 0.001 | |
| Significance of all canonical axes | 0.07 | | 0.001 | |

UVC clusters were more organized compared to catches and also divided the sampling month into three distinct groups (Fig. 5). The first group was represented by 10 months of Bandrélé followed by two months of Dzoumogné (May and February) and one month of Malamani (November). The second group gathered three sampling months of Malamani (January, March and April) and one month of Dzoumogné (January). The third group was composed principally by sampling months of Dzoumogné (10), Malamani (9) and only three months of Bandrélé (March, April and June). The first groups gathered the highest abundance of fishes for Bandrélé, the second group for Malamani and the third group for Dzoumogné.

The relationship between reef fish assemblages and the environmental descriptors influencing their spatial distribution were performed using canonical RDA analysis triplot (Fig. 6). Table III provides RDA results for the abundance between sampling methods and the two first axes. The RDA revealed that the environmental variables explained 26.5% of the variation in the species abundance data for catches and 37.1% for the UVC (Tab. III). Overall permutation test on the first two axes showed that the canonical significance correlation between fish assemblages and environmental variables was highly significant ($p = 0.001$) for the UVC but not for the catches ($p = 0.07$). The RDA results showed that the most significant factors explaining variation in community structure were temperature, reef proximity and fishing time for the catches. The same trend was observed for UVC, although temperature, water transparency and reef proximity were the most significant factors. These three variables explained 18.5% and 26% of the variation in the species matrix for catches and UVC respectively as well as 69.8% and 70.1% of the species-environment relationship (Tab. III). For the catches, the two first axes explained 18.4% of the canonical analysis on the abundance data (Fig. 6A). The first axis opposed the sampling months with higher fishing time ($r = 49.4$) and closer to the reef ($r = 34.8$) to the sampling months located in proximity to the river ($r = 35.2$). The second axis was mainly characterised by the variable "temperature" ($r = -50.2$), opposed the sampling months carried out in wet and dry season (Fig. 6A).

Concerning the second RDA performed on the abundance data from UVC, a total of three variables were significant and the first two axes explained 26% of the total variance (Fig. 6B). Conversely of canonical RDA of the catches, the results obtained from UVC data showed a clear opposition along the first axis.

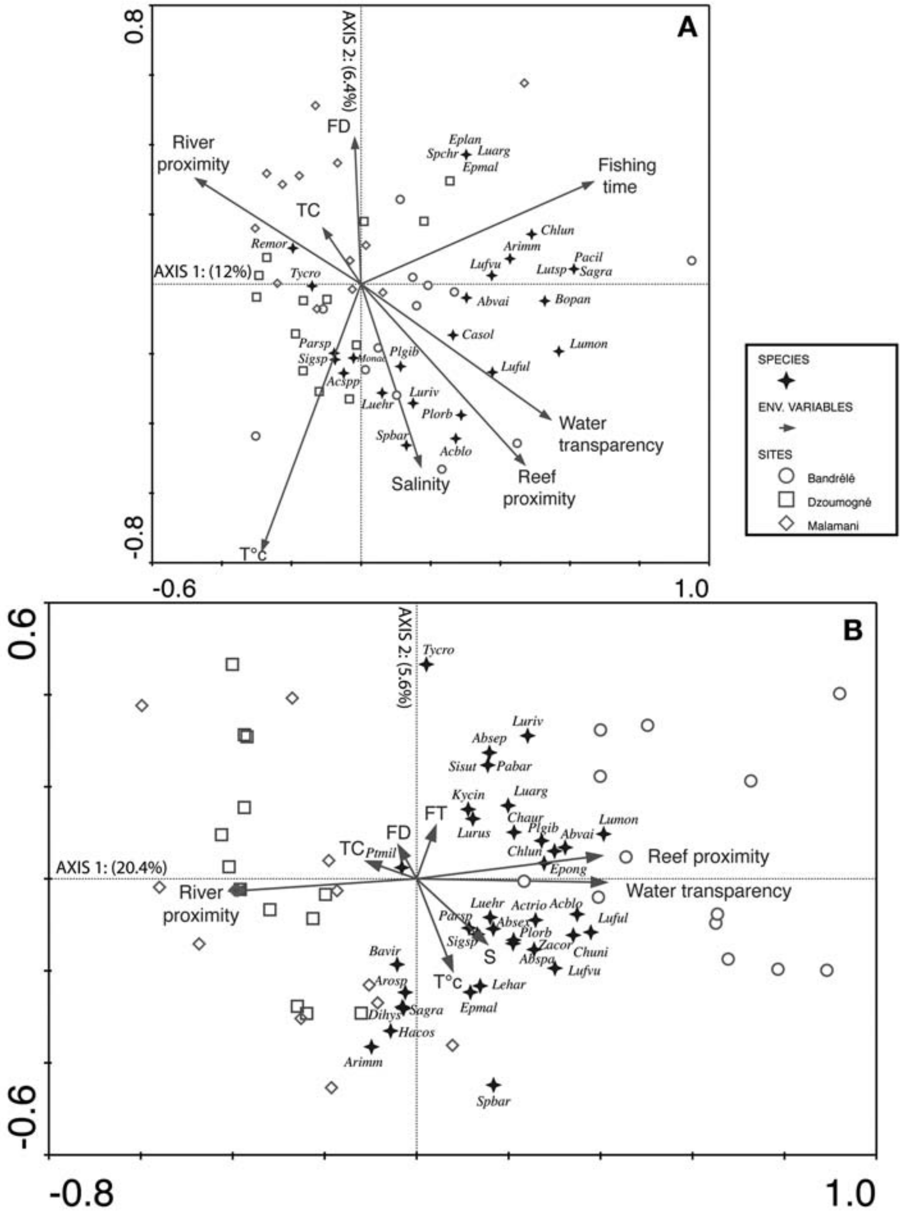

Figure 6. – Canonical redundancy analyses (RDA) of fish abundance, environmental variables and sampling months for catches (**A**) and UVC (**B**). Species are coded by the two first letters of name of genus and the three first letters of species, these codes are given in table I.

This axis opposed the sampling months of Bandrélé located near coral (r = 78.3), characterised by clear water (r = 80.2) and those from Dzoumogné and Malamani located near a river (r = –79). Bandrélé harboured mostly reef fish species sampled in the mangrove. As with catches, the second axis was significantly associated with temperature (r = –66) and marked the seasonal difference (Fig. 6B).

## Temporal variation in total fish abundance and species richness

Species richness varied over the year with a marked decrease during the dry season for all sites except Bandrélé mangrove, which had a high number of species (Fig. 7). The seasonal variation in species richness was significantly higher in wet season (Wilcoxon signed-rank test; $p = 0.026$) for UVC and did not vary significantly ($p > 0.05$) for catches (Fig. 7A, B). In Bandrélé, one important peak of species richness was observed at the end of dry season (in September) for both sampling methods (Fig. 7). This peak corresponded with the abundance of nine families from UVC, eight families from catches, with Lujanidae family as the most diverse for both techniques. Others small peaks were observed in the wet season for catches in Bandrélé (in December and February) and in Dzoumogné (in March). On the other hand, one important peak was observed in January during the wet season in Bandrélé and Malamani for UVC.

Concerning variation of fish abundance among seasons, there were no significant differences for catches between dry

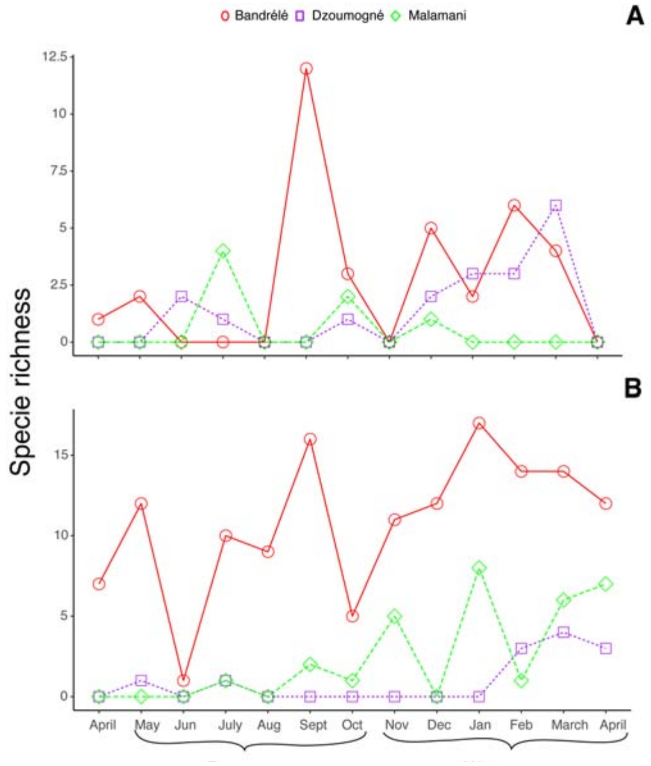

Figure 7. – Temporal variation in total species richness in three mangrove habitats for catches (**A**) and UVC (**B**).

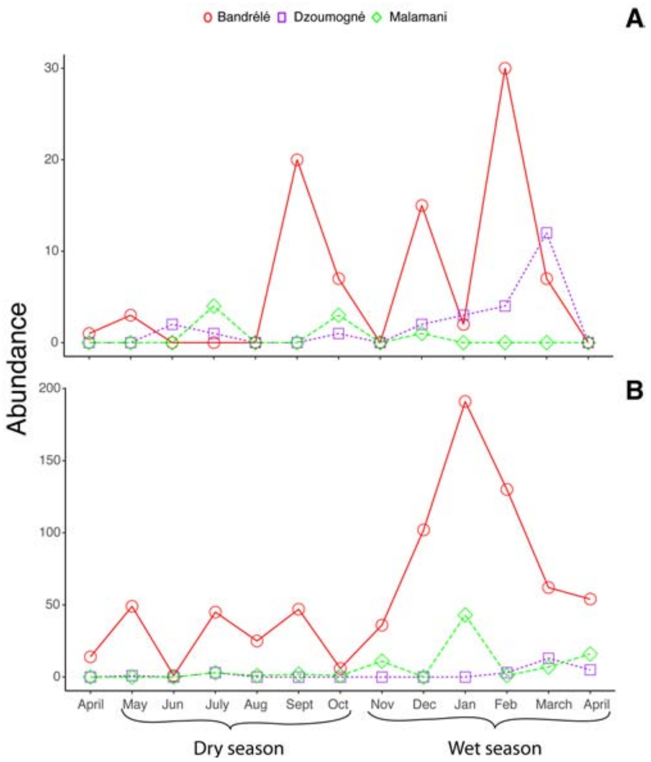

Figure 8. – Temporal variation in total abundance in different mangrove habitats for catches (**A**) and UVC (**B**).

and wet season (Fig. 8A). Fish abundance was found in significantly high number in wet season compared to dry season (Wilcoxon signed-rank test; p = 0.012) for UVC (Fig. 8B). Most abundance variation in catches was found in Bandrélé where three high peaks (in September, December and February) were observed. These were due to a juvenile dominance of *Lutjanus monostigma* in September, *L. fulviflamma* in December, *Acanthurus blochii* and *Sphyraena barracuda* in February. Difference in fish abundance was very marked for UVC in wet season with one important peak in January for Bandrélé and also a small peak for Malamani (Fig. 8b). In Bandrélé, this peak was explained by high number of juveniles of *Abudefduf sparoides* and *A. vaigiensis*, *Acanthurus blochii*, *Lutjanus ehrenbergii*, *L. fulviflamma* and *L. monostigma*. Juveniles of *Sphyraena barracuda* and adults of *Lutjanus fulviflamma* were responsible of this peak observed in Malamani.

## DISCUSSION

Reef fish community is spatially differentiated between three mangrove habitat types: Bandrélé near the coral reef, Dzoumogné near a river and Malamani in a bay, the last two having estuarine influence. Descriptors (species richness and abundance) showed higher values in mangrove near the coral reef than those with estuarine influence. Concerning temporal variations, the structure of reef fish varied significantly among seasons. The present study found that mangroves in close proximity to reefs were important for juveniles and suggests that environmental variables have an impact on the habitat accessibility.

In this study, underwater visual census (UVC) has been found to be more effective in assessing reef fish abundance in mangrove than fyke-net. This nondestructive method, the advantages and disadvantages of which have been discussed in different papers (Harmelin-Vivien *et al.*, 1985; Harmelin-Vivien and Francour, 1992; English *et al.*, 1997) allowed to sample more individuals and species. This was true for Bandrélé, where water transparency (> 1 m) facilitated the visual sampling in the mangrove, where 761 individuals comprising 35 reef species has been recorded and I suggest that one fyke-net is not sufficient to sample mangrove habitats. Despite numerous reef species found in non-estuarine mangrove (Bandrélé) in this study, few species are common to mangrove and reef habitats when comparing different lists of species available for reef habitats in Mayotte (Letourneur, 1996a; Chabanet, 2002; Madi Moussa *et al.*, 2015). While about half of the families are common to reefs, only 3.1-12% of total species richness is found on both habitats. For example, seven species, *Abudefduf sexfasciatus*, *A. sparoides*, *A. vaigiensis*, *Acanthurus triostegus*, *Canthigasther solan-*

*dri*, *Halichoeres cosmetus* and *Kyphosus* sp., were similar to those observed in coral reef by Chabanet (2002). In the Indo-Pacific region, numerous studies have reported that few juvenile reef fish species are observed in both mangrove and reef habitats (Thollot and Kulbicki, 1988; Thollot, 1992; Dorenbosch *et al*., 2005; Unsworth *et al*., 2009; Barnes *et al*., 2012; Honda *et al*., 2013; Madi Moussa and Galzin, 2013). Changes in environmental variables such as salinity, temperature and turbidity have been identified as the most important factors that may limit fish assemblage interactions between habitats (Benfield and Minello, 1996; Methven *et al*., 2001; Barletta *et al*., 2005; Vaslet *et al*., 2010). Tidal regime also appears to act as an important driver of fish distributions and can have a profound influence on habitat accessibility (Unsworth *et al*., 2007; Igulu *et al*., 2014). In Mayotte, distance between mangrove and adjacent habitats with the ebbing tide seems to be important in terms of energy for small juvenile fishes, of which long-distance migration may increase predation risk and energy cost. In contrast, "transient" species are large individuals that have good swimming abilities to move quickly and efficiently escape predators (Doherty, 2002), frequent in these mangroves. Salinity is often suggested as an important variable to explain spatial differences between mangrove fish communities close to the mainland and those located near the reef. In this study, reef fish distribution in the mangroves can be explained by environmental (water transparency, temperature) and spatial variables (distance to the reef). The low species richness and abundance in mangroves under estuarine influence are probably due to low water transparency and far distance from reef. With relatively stable salinity values in all sites, 29 and 35.5, the other factors (water transparency, distance to the reef and temperature) are much more important in explaining the distribution of juvenile reef fishes in mangrove.

Several authors have argued that foraging may be an important activity in mangrove habitats and food availability influences fish distributions (Nagelkerken and Van der Velde, 2004; Lugendo *et al*., 2006, 2007). In this study, first order carnivores, zooplanktivores and herbivores were the most abundant feeding guilds in Bandrélé where piscivores were less represented. Second order carnivores dominated in Dzoumogné whereas piscivores were dominant in Malamani bay mangroves. This observation is contrary to what has been reported from some other tropical regions, where predation can be very intense in clear water, whereas turbid waters provide greater safety for juveniles (Blaber, 1986). This suggests that turbidity can reduce the feeding activity of piscivores, which depend on visual cues to feed (Benfield and Minello, 1996). Their statement was not born out by this study, where Bandrélé was characterized by clear water and less represented by piscivores whereas Dzoumogné and Malamani, which were influenced by turbid water, harboured an important proportion of piscivores. Further research is required to determine if reef fishes that are observed to inhabit mangrove habitats use these areas as foraging grounds rather than shelter. Unsworth *et al*. (2009) suggest refuge from predation is likely to be of greater importance to smaller fish within these habitats. The abundance of juveniles observed (81% from UVC and 93.5% of catches) during this study was high in comparison to the abundance of adults. The median size of six dominant species (*Abudefduf sparoides*, *Abudefduf vaigiensis*, *Acanthurus blochii*, *Lutjanus fulviflamma*, *L. monostigma* and *Sphyraena barracuda*) observed in the mangroves was smaller (7-7.9 cm). To reduce predation pressure, smaller fish preferentially utilise the mangrove habitat due to the habitat complexity (Nagelkerken and Van der Velde, 2004).

Among the six species, some may be dependent on mangroves during their juvenile stage and moved definitively to adjacent habitat (*e.g*. coral reefs) when they reached maturity. Moreover, some fishes may exhibit two habitat use strategies with a possible ontogenetic habitat shift from mangrove to seagrass and coral reefs (Kimirei *et al*., 2011; Honda *et al*., 2013) *e.g*. *Lethrinus harak*, *Lutjanus fulviflamma*, *L. fulvus, L. monostigma*, *Parupeneus barberinus*, *Siganus* sp. The juvenile of *Sphyraena barracuda,* whose adults were present on coral reefs, may be dependent on mangroves or seagrass as nursery habitat as suggested by Nagelkerken *et al*. (2002). In Mayotte, there is no mangrove adjacent to seagrass beds and all fish species using mangrove as feeding or shelter habitats must migrate to the sand/mud flats, river channels or coral reefs during low tides. These findings suggested, therefore, that the mangrove habitats in the present study sites have a nursery function for these fishes (Beck *et al*., 2001).

A finding of the present study indicates the existence of temporal variation in reef fish community in the mangrove. Fish descriptions varied seasonally, the largest numbers of species and individuals were observed during rainy season and the lower abundances between May and October in dry season. These observations are consistent with the previous findings in subtropical mangroves in eastern Australia, where abundances and species richness peak in summer and are low in winter (Laegdsgaard and Johnson, 1995). The present study showed that juvenile reef fishes revealed peaks of abundance between December and February with one important in January. In their study on Great Barrier Reef, Russell *et al*. (1977) found juvenile peaks of abundance in January-February when temperatures are highest. Water temperature was identified as an important factor structuring the temporal variations of juvenile reef fishes in mangroves. According to Abesamis and Russ (2010), environmental variables such as temperature and wind have a significant effect on the patterns of reef fish recruitment. They suggested that the best moment of settlement of larvae within the year is during a 4-6 month period when water temperatures are warmest and when winds are weakest. The same trend was observed by Letourneur (1996b) at Reunion Island, where high rates of recruitment were observed during the summer periods characterized by calm hydrodynamic conditions. This period, corresponding to the greatest primary production, can enhance growth rates of larval reef fishes and ensure that larval metamorphosis occur at the right time of year (Russell *et al.*, 1977).

This study revealed that mangroves were found to be important habitat for juveniles of some reef fish species, thus supporting the hypothesis of a nursery function and which have a similar role to mangroves in the Caribbean region (Nagelkerken *et al.*, 2000b; Dorenbosch *et al.*, 2004a). Nevertheless, the nursery value of mangrove habitats for reef fishes appears to relate to site, environmental variables, food availability and seasonal factor. The important number of reef species and abundance in Bandrélé mangroves may be explained by environmental variables such as water transparency, reef proximity facilitating habitat accessibility, salinity, temperature and food availability. First order carnivores, zooplanktivores and herbivores were mainly observed in Bandrélé, whereas piscivores were dominant in Malamani mangrove and second order carnivores were well represented in Dzoumogné site. Also, foraging ground appears to be a more important factor than a nursery area for most reef fishes recorded in mangroves, which could be a result of tidal migration (Unsworth *et al.*, 2007; Madi Moussa *et al.*, 2015). Further study must be undertaken to confirm this hypothesis. However, integrating this area in a marine reserve may have an ecological importance in habitat connectivity and promote reserve performance (Olds *et al.*, 2012).

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